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Hyopsodus (Mammalia) from the Tepee Trail Formation (Eocene), Northwestern Wyoming

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ABSTRACT

Two species of *Hyopsodus* are recognized from the Tepee Trail Formation in its type area of northwestern Wyoming. The two species do not occur together. *Hyopsodus* sp. cf. *H. paulus* is found lower in the Tepee Trail Formation than is the new species, *Hyopsodus lovei* which is found in Bone Bed A of the type section (Love, 1939). *Hyopsodus lovei* is distinguishable from all other species of *Hyopsodus* by the presence of a unique lower incisor battery, and several other dental features. *Hyopsodus paulus* is known predominantly from Bridgerian Land Mammal Age strata elsewhere, although it does range into the Uintan; *H. lovei* is known only from Shoshonian Subage (earliest Uintan Land Mammal Age, Middle Eocene) strata of northwestern Wyoming.

INTRODUCTION

Mammalian faunas in the Tepee Trail Formation have been known since the original naming and description of the formation (Love, 1939). In fact, Love (1939) designated the type section of the Tepee Trail Formation in a section that contained mammal-bearing strata, even though more complete sections were exposed nearby. Love's foresight has facilitated precise geochronologic studies and correlation of the Tepee Trail Formation by subsequent workers (e.g., McKenna, 1980, 1990; Flynn, 1986). Because of the extremely hard matrix encasing the mammalian fossils, fossil discovery, preparation, and study is a time-consuming process. However, many of the specimens preserve exquisite anatomical detail. Following 20 years of patient collecting by M. C. McKenna, enough material was available to permit preparation of a preliminary faunal list for the Tepee Trail Formation (McKenna, 1972, 1980). Detailed description of the individual taxa in this important fauna will be a continuing process (Rose, 1978; MacFadden, 1980; Flynn and Galiano, 1982; this paper; McKenna, 1990).

Hyopsodus is an important taxon in many

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Eocene faunas. It first appeared in the North American record in the Wasatchian (or latest Clarkforkian, based on two specimens, Rose, 1980). *Hyopsodus* was most diverse and abundant in the Wasatchian and Bridgerian, and continued into the Uintan and Duchesnean in reduced numbers and diversity. Because of their abundance, diversity, relatively short temporal duration, and wide geographic range, species of *Hyopsodus* are important in defining Eocene biochronologic intervals. *Hyopsodus,* however, has had a confusing taxonomic history (see below). West (1979) and Krishtalka (1979) revised the Bridgerian and Uintan/Duchesnean species of *Hyopsodus,* respectively. These studies have been invaluable in my analysis of the Tepee Trail Formation *Hyopsodus.*

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, New York
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.
CM	The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

Acknowledgments

I thank J. David Love for his enthusiasm, intellect, assistance, and insight into geologic problems. Malcolm C. McKenna has provided encouragement and an extensive collection of fossils from the Tepee Trail Formation. Numerous graduate students, field assistants, and visitors provided the labor to produce the Tepee Trail fossils. I especially thank Otto Simonis for his patient and caring preparation of these difficult specimens over many years. Jean Kelly and M. Feldmann, American Museum of Natural History, generously helped me with the molding and casting of specimens. Marlene Werner-Hill prepared the invaluable illustrations. I thank Mac West, Richard Stucky, and Michael Novacek for their reviews, which improved the manuscript.

PREVIOUS TAXONOMIC STUDY

Hyopsodus has had a confusing taxonomic history; defining species and determining their phylogenetic interrelationships has proved particularly problematic. Many of these difficulties stem from "gradual acquisition of derived dental characters and shifts in frequencies and degrees of expression of these characters through time" (Redline, 1989). Most studies have used dental size as the primary distinction between species, with subjective division of seemingly continuous morphologic variation used to distinguish major subsets of species (generally temporal clusters of species, e.g., "Bridgerian *Hyopsodus*"). Similar difficulties were encountered within this study. Although some characters appear to be acquired through stabilization of intraspecific variation within clades, many of the Uintan and Duchesnean species and clades can be clearly diagnosed by at least a few discrete, unique apomorphies.

Gazin (1968) provided the most extensive revision of *Hyopsodus.* In that study he recognized 12 valid species of *Hyopsodus,* all of which were considered restricted to one of the Eocene North American Land Mammal Ages (5 Wasatchian, 5 Bridgerian, 2 Uintan). Gingerich's (e.g., 1974, 1976, 1980) stratophenetic studies of Wasatchian *Hyopsodus* in the Bighorn Basin of Wyoming led him to recognize all five of Gazin's (1968) Wasatchian species, to resurrect five species placed in synonymy by Gazin (1968), and to name a new species. West (1979) revised the systematics of Bridgerian *Hyopsodus,* recognizing only three valid Bridgerian species. West (1979) mainly used molar size differences (and secondarily, stratigraphy) to distinguish the species. West (1979) also proposed a number of discrete, derived characters that distinguished all Bridgerian species from all Wasatchian species of *Hyopsodus,* although he recognized that some of these characters represented further elaboration or modification of conditions already existing within some Wasatchian species (e.g., "increased lophodonty," "more complete development of the trigonid on p4," West, 1979: 5). Krishtalka (1979) revised the systematics of "late Eocene" (Uintan and Duchesnean) *Hyopsodus,* synonymizing one of Gazin's (1968) two valid Uintan species (*H. fastigatus*) with the other (*H. uintensis*), and naming a new Duchesnean species (*H. sholemi*) for some of the material that previously had been assigned to *H. "fastigatus."* Redline (1989, and Ph.D.

in progress) is revising the systematics of early Eocene (Wasatchian and early Bridgerian) *Hyopsodus,* recognizing four or five "anagenetically evolving species-lineages" (Redline, 1989). A brief summary of the taxonomy and systematics of currently recognized Bridgerian to Duchesnean species of *Hyopsodus* (following Gazin, 1968; West, 1979; Krishtalka, 1979) is presented as a prelude to the analysis of the Tepee Trail *Hyopsodus* material.

CONDYLARTHRA COPE, 1881

HYOPSODONTIDAE TROUESSART, 1879[2]

Hyopsodus Leidy, 1870
Synonyms: (?) *Stenacodon* Marsh, 1872; *Lemuravus* Marsh, 1875
Type Species: *Hyopsodus paulus* Leidy, 1870

Hyopsodus paulus Leidy, 1870
Synonyms: (?) *Stenacodon rarus* Marsh, 1872; *Lemuravus distans* Marsh, 1875; *Hyopsodus vicarius* (Cope), 1873; *Hyopsodus marshi* Osborn, 1902; *Hyopsodus despiciens* Matthew, 1909; *Hyopsodus markmani* Abel and Cook, 1925
Known Temporal Range: Bridgerian to early Uintan

Hyopsodus minusculus Leidy, 1873
Known Temporal Range: Bridgerian

Hyopsodus uintensis Osborn, 1902
Synonyms: *Hyopsodus fastigatus* Russell and Wickenden, 1933
Known Temporal Range: Uintan

Hyopsodus lepidus Matthew, 1909
Known Temporal Range: Bridgerian

Hyopsodus sholemi Krishtalka, 1979
Known Temporal Range: Uintan

Hyopsodus tonksi Eaton, 1982
Known Temporal Range: Bridgerian

Hyopsodus lovei, new species
Known Temporal Range: earliest Uintan (Shoshonian Subage)

[2] As discussed in footnote 5 of Gazin (1968), Trouessart (1879) provided the first usage within the family group of a name derived from *Hyopsodus*—"Hyopsodinae," although the current spelling of the family name follows the usage first proposed by Lydekker (in Nicholson and Lydekker, 1889: 1465).

SYSTEMATICS

CONDYLARTHRA COPE, 1881

HYOPSODONTIDAE TROUESSART, 1879

HYOPSODUS LEIDY, 1870

Hyopsodus lovei, new species
Figures 1–9

HOLOTYPE: AMNH 96295 (fig. 1), partial left and right mandibles with right i2, p3–4, and left i1–2; Bone Bed A of Love (1939), Tepee Trail Formation.

TYPE LOCALITY: Bone Bed A of Love (1939), type section of the Tepee Trail Formation, East Fork Basin, 27 km northeast of Dubois, northwest part of the Wind River Basin, Fremont County, Wyoming.

AGE: Shoshonian Subage, earliest Uintan Land Mammal Age (middle Eocene—see Flynn, 1986; McKenna, 1980; Berggren et al., 1978).

REFERRED MATERIAL: AMNH 88290 (left maxillary fragment; M2–3; fig. 8), 96264 (right mandible; p2–m3; alveoli for i3, c, p1; fig. 4), 96395 (right mandible; p4–m1), 97261 (left mandible; p4–m1; fused symphysis), 98084 (left maxilla; I2–3, C, P2–4, M1–3; fig. 7), 99147 (left mandible; p2–m3; alveoli for i2–3, c, p1; fused symphysis; posterior ramus; fig. 2), 99154 (left maxillary fragment; P3–4, M1), 101958 (right mandible; p3–m1), 104703 (right M1or2), 104876 (left mandible; p2–m3; possibly associated with isolated fragment of ?right mandible with i2; figs. 6, 9), 108016 (left mandible; p3–m1; p2, crown broken; alveoli for c, p1), 108017 (left mandible; m2–3), 113923 (m1or2), 113944 (left maxilla; P2–M3; fig. 7), 114018 (p3–m3), 114057 (right mandible; p2–m3; fig. 5), 116454 (right mandible; i2–3, p2–m1; fig. 3); all from Bone Bed A of the type section of the Tepee Trail Formation.

ETYMOLOGY: Named for Dr. J. David Love, in honor of his original discovery of the Bone Bed A locality, his contagious enthusiasm, and his continued interest in the geologic history of the Absaroka Range.

DIAGNOSIS: A species of the genus *Hyopsodus* that differs from all other species of *Hyopsodus* in the (1) closely appressed antemolar dentition; (2) short, robust mandible; (3) broad, anteroposteriorly short, more triangular (in outline) shaped p3–4 with very

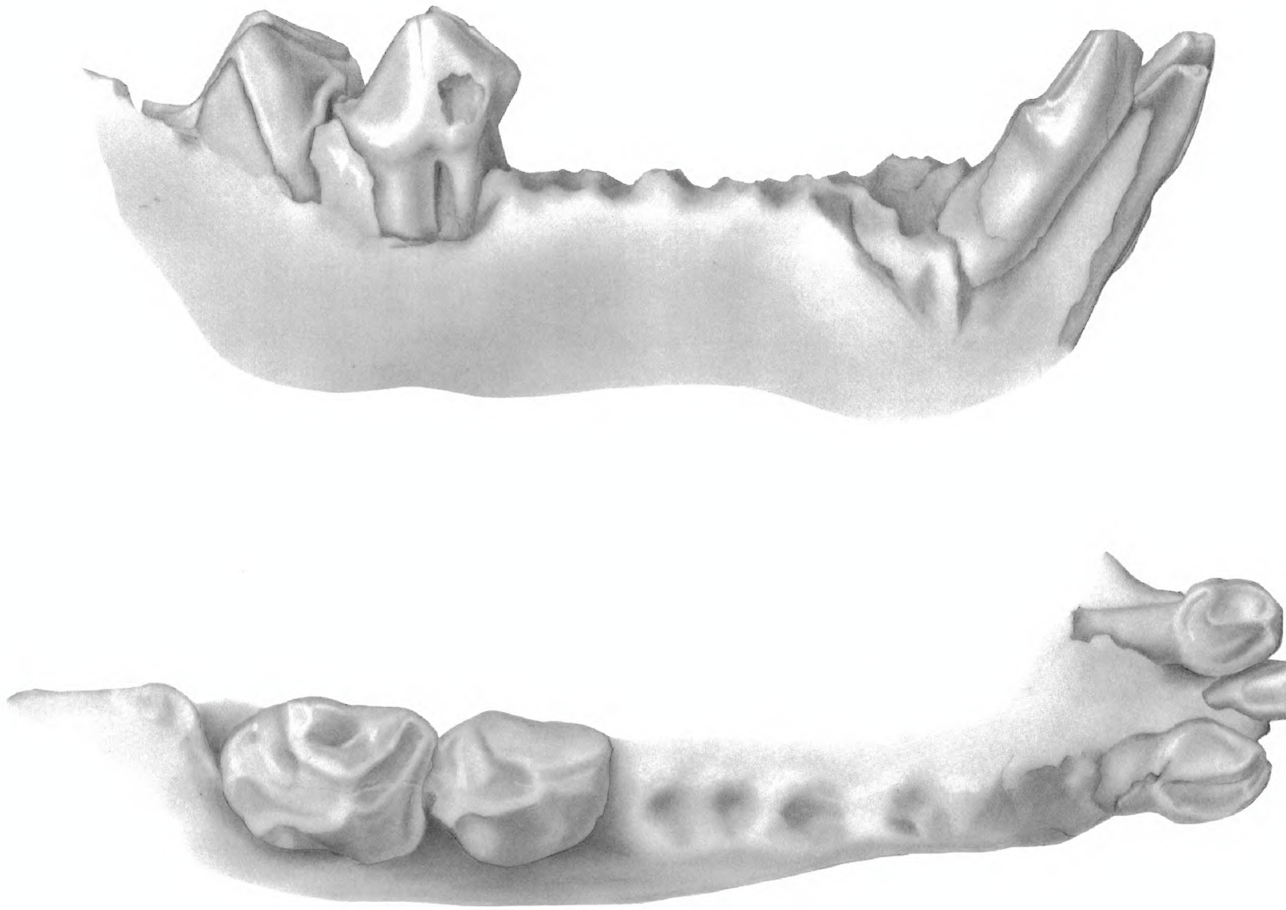

Fig. 1. Type specimen, AMNH 96295. Mandibles with right i2, p3–4 and left i1–2. (**Top**) labial view, (**bottom**) crown view. 8.0×.

short (anteroposteriorly) talonids and transversely expanded tooth crowns just posterior to the protoconid apex; (4) relatively broader than long p4, much lower length/width ratio; (5) broad slope or shelf on the labial side of p4 (labial to the centrally located paralophid and cristid obliqua); (6) oblique, rather than squared, posterolabial margin of p4 talonid; (7) development of an unique incisor dental battery (described below).

Hyopsodus lovei differs from *H. paulus* and all other previously described species of Wasatchian and Bridgerian *Hyopsodus* in the unique diagnostic features cited above, in its larger size, in dental proportions (see discussion) and in the presence of the synapomorphies *H. lovei* shares with *H. uintensis* and *H. sholemi* (node B, fig. 10 and character list).

Hyopsodus lovei lacks the synapomorphies shared by *H. uintensis* and *H. sholemi* (node C, fig. 10 and character list), as well as the autapomorphies of each of those species (nodes E and F, fig. 10 and character list). *H. lovei* is smaller than *H. sholemi*. *H. lovei* also differs from *H. uintensis* and *H. sholemi* in dental proportions (see discussion).

DESCRIPTION: The upper molars of *H. lovei* have an angular, relatively squared outline. Lophodonty is well developed, and the ectoloph is sharp, high and "wall-like." The cusps are high crowned and relatively trenchant. The hypocone is large and there is a

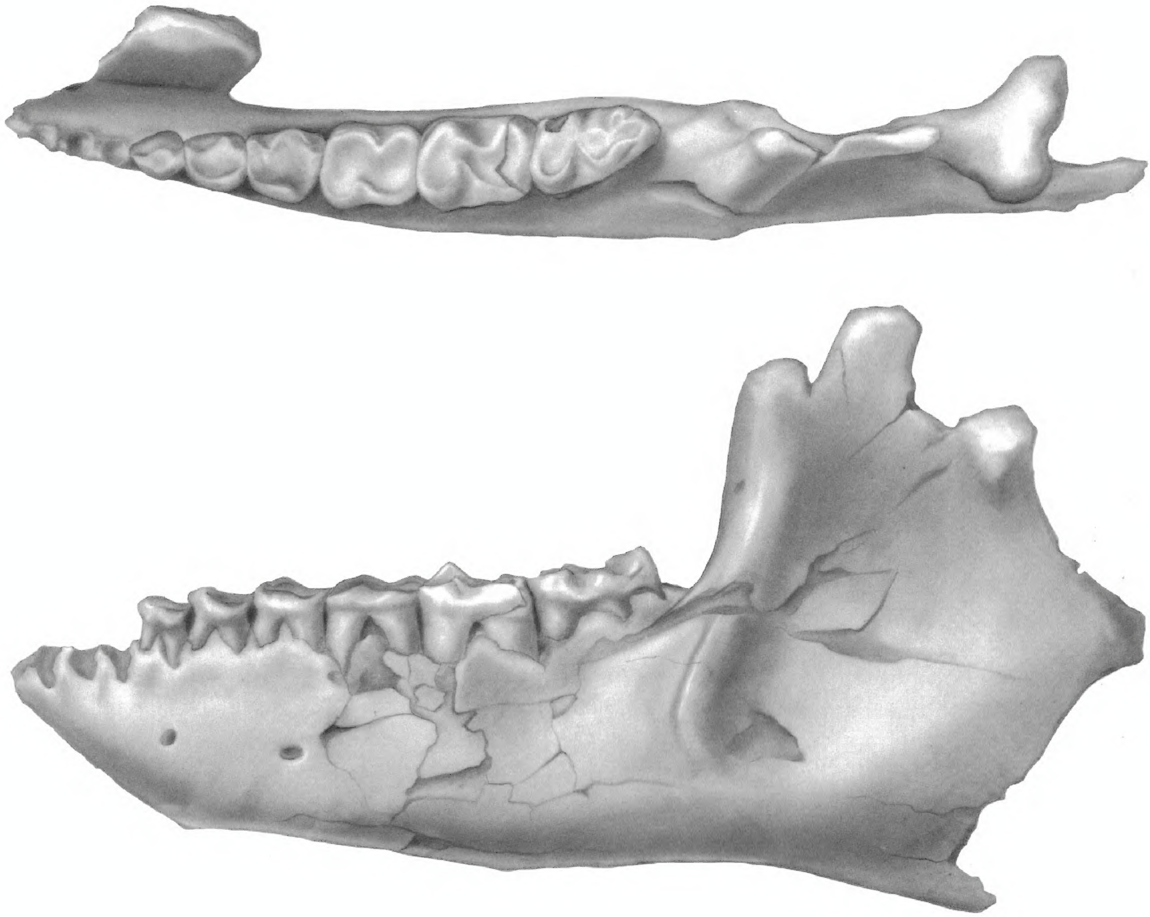

Fig. 2. AMNH 99147. Left mandible, p2–m3. (**Top**) crown view, (**bottom**) labial view. 2.1×.

deep lingual valley between the hypocone and protocone. However, there is a strong ridge connecting the hypocone and protocone, and the lingual valley is not continuous to the center of the tooth. M2 is larger than M1, and M1 is larger than M3 (see table 2).

The labial tooth margin is oriented slightly obliquely (slants anterolabially to posterolingually) on M3. The hypoconal shelf on M3 is relatively broad and a hypocone is variably developed as a distinct cusp on the posterior cingulum. A strong, sharp parastyle wing projects anteroexternally on M2, and the labial margin of M2 is relatively oblique.

P4 has a strong preprotocrista, broad postcingulum and a "swelling" of the enamel in the paraconule region. A well-developed parastyle wing projects anterolabially.

P3 also has a strong preprotocrista and broad postcingulum, but has no indication of the elaboration of a paraconule. The protocone is situated anterior to the paracone apex. The P3 is generally triangular in outline. A high, robust, bulbous paracone and a lower protocone dominate the P3 crown. A deep valley separates the protocone from the paracone. The metastyle region is small and poorly elaborated.

A single, large main cusp dominates the crown of P2. This cusp is anteroposteriorly elongate and transversely narrow. A sharp ridge extends from the posterolabial edge of P2, to the apex of the main cusp, and then to the anterolingual edge of the tooth, which makes P2 a relatively trenchant tooth.

None of the available specimens of *H. lovei* preserves P1, although an alveolus for this tooth is present in AMNH 98084.

TABLE 1
Measurements (mm) of Lower Dentitions of *Hyopsodus lovei* from Bone Bed A, Tepee Trail Formation, East Fork Basin Area, Wyoming

													Hyopsodus lovei			*H.* cf. *paulus*	
													Bone Bed A sample				
	AMNH 99147	AMNH 96264	AMNH 104876	AMNH 108016	AMNH 101958	AMNH 96395	AMNH 108017	AMNH 97261	AMNH 116454	AMNH 114018	AMNH 114057	AMNH 96265	N	Mean	Obs. Range	AMNH 104751	AMNH 104752
p2 L	2.469	2.209							2.198		2.119		4	2.249	2.12–2.47		
W	2.263	2.017							1.735*		1.873		3	2.051	1.87–2.26		
p3 L	3.009	2.715	2.632	3.042*	2.989				2.802	3.030*	3.159	2.761	7	2.871	2.63–3.19		
W	2.796	2.482		2.647	2.435				2.307	2.533	2.573	2.348	8	2.515	2.31–2.80		
p4 L	3.536	3.362	3.417	3.579	3.538	3.757		3.858	3.382	3.754	3.520	3.388	11	3.554	3.36–3.86		3.065
W	3.238	3.000	2.909	2.968	3.030	3.310		2.591	2.891	3.127	3.033*		9	3.007	2.59–3.31		2.592
m1 L	4.244	4.672	4.511	4.783	5.052	4.797		4.829	4.854	4.373	4.809		10	4.692	4.24–5.05	4.166	4.255
Wa	3.550	3.805	3.440	3.357	3.696	3.720		3.506	3.434	3.373	3.491		10	3.537	3.36–3.81	2.790	2.964
Wp	3.693	3.778	3.602	3.637	3.882	3.818		3.507	3.684*		3.642		8	3.695	3.51–3.88	3.011	3.321
m2 L	5.027	4.893	4.756				5.076			5.168	5.006		6	4.988	4.76–5.17	3.945	
Wa	4.081	3.771	3.822				3.248			3.624	3.711		6	3.710	3.25–4.08	3.228	
Wp	3.951	3.741	3.852				3.272			3.761	3.514		6	3.682	3.27–3.95	2.991	
m3 L	5.728	5.220								5.715*	5.244		3	5.397	5.22–5.73		
Wa	3.649	3.129	3.381							3.204	3.263		5	3.325	3.13–3.65		
Wp	3.220	2.545								2.894	2.772		4	2.858	2.55–3.22		
p2–m3	23.255	21.506															
p4–m3	18.015	17.018															

AMNH 113923 (m1 or m2) L 4.971, Wa 3.754, Wp 3.658.
Asterisks (*) refer to best approximation measurements for broken or distorted teeth; these measurements were not used in calculations of sample means.

The upper canine is somewhat squared in crown outline, and, when viewed from the posterolingual side of the tooth, has a triangular profile (triangle apex at the apex of the main cusp). The canine crown is dominated by a single, large main cusp. This cusp comes to a sharp peak at its apex, and the anterolabial slope of this cusp is bulbous. A sharp ridge extends from the anterolingual to the posterolabial edge of the upper canine, as in P2, and the tooth is relatively trenchant. A very weak posterolingual cingulum is present.

In shape and morphology I2–3 are very similar to the upper canine. However, the main cusp on I3 is a little higher than on C, and the axis of the sharp, anterolingual to posterolabial ridge is aligned more anteroposteriorly on I2–3 than on C.

The upper incisors and canine are relatively widely separated in the maxilla.

The mandibular symphysis is tightly fused and strong, and extends posteriorly beneath the anterior margin of p3. The mandible is robust, relatively deep, broad mediobuccally, and curved on its ventral border. The mandibular ramus is very broad and deep; the ascending ramus is almost vertical and it lies near the buccal edge of the tooth row. Both the anterior and posterior borders of the coronoid process are vertical, and the process is relatively narrow anteroposteriorly. The masseteric fossa is relatively deep, is bordered anteriorly by a strong coronoid crest, and extends anteriorly only to below the posterior edge of m3. The condyle is broad and rounded, and it lies well dorsal to the level of the tooth row and well anterior to the posterior border of the angular process. Its long axis is oriented slightly obliquely (anterolabially to posteromedially), and there is a small posteromedial process that is inflected ventrally. Abrasion and breakage of the dorsal surface of the condyle obscures the nature of most of the articular surface, although some articular wear is preserved on the ventrally projecting surface of the small posteromedial process. Although broken, it is clear that the

TABLE 2
Measurements (mm) of Upper Dentitions of *Hyopsodus lovei* from Bone Bed A, Tepee Trail Formation, East Fork Basin Area, Wyoming

	AMNH 98084	AMNH 99154	AMNH 88290	AMNH 104703	AMNH 113944	*Hyopsodus lovei* Bone Bed A sample		
						N	Mean	Obs. Range
P2 L					2.031	1	2.031	–
W					1.942	1	1.942	–
P3 L	3.084	3.001*			2.547*	1	3.084	–
W	3.697				3.130*	1	3.697	–
P4 L	3.412*	3.171			2.974*	1	3.171	–
W	5.194	5.226			4.058*	2	5.210	5.19–5.23
M1 L	4.347	4.374		4.558	4.495*	3	4.426	4.34–4.56
Wa	5.758	5.682		5.524	4.864*	3	5.655	5.52–5.76
Wp	5.835	5.475		5.660	4.836	4	5.452	4.84–5.84
M2 L	4.965		4.660		4.411	3	4.679	4.41–4.97
Wa			5.820		5.759	2	5.790	5.76–5.82
Wp			5.704		5.494	2	5.599	5.49–5.70
M3 L	3.893		3.742		3.466	3	3.700	3.47–3.89
Wa	5.341		4.845		4.429	3	4.872	4.43–5.34
Wp			4.718			1	4.718	–
P4–M3	16.057							
M1–3	12.471							

TTA '77 (AMNH Unnumbered): M upper: L 4.004, Wa 4.257, Wp 4.231.

Asterisks (*) refer to best approximation measurements for broken or distorted teeth; these measurements were not used in calculations of sample means.

TABLE 3
Ratios of Length/Width for Lower Dentitions of Species of *Hyopsodus*

	lovei (1)	cf. *paulus* (2)	*uintensis* (3)	*sholemi* (4)	*tonksi* (5)	*minusculus* (6)	*paulus* (7)	*lepidus* (8)
p2 L/W	$\frac{2.249}{2.051} = 1.10$							
p3 L/W	$\frac{2.871}{2.515} = 1.14$							
p4 L/W	$\frac{3.554}{3.007} = 1.18$	$\frac{3.065}{2.592} = 1.18$	$\frac{3.5}{2.817} = 1.24$	$\frac{4.2}{3.3} = 1.27$		$\frac{2.42}{1.92} = 1.26$	$\frac{3.41}{2.67} = 1.28$	$\frac{3.08}{2.49} = 1.24$
ml L/Wa	$\frac{4.692}{3.537} = 1.33$	$\frac{4.211}{2.877} = 1.46$				$\frac{3.13}{2.45} = 1.28$	$\frac{4.16}{3.17} = 1.31$	$\frac{3.69}{3.02} = 1.22$
ml L/Wp	$\frac{4.692}{3.695} = 1.27$	$\frac{4.211}{3.166} = 1.33$	$\frac{4.5}{3.318} = 1.36$		$\frac{3.89}{2.935} = 1.33$	$\frac{3.13}{2.44} = 1.28$	$\frac{4.16}{3.31} = 1.26$	$\frac{3.69}{3.28} = 1.13$
m2 L/Wa	$\frac{4.988}{3.710} = 1.34$	$\frac{4.194}{3.448} = 1.22$				$\frac{3.28}{2.70} = 1.22$	$\frac{4.28}{3.61} = 1.19$	$\frac{4.24}{3.46} = 1.23$
m2 L/Wp	$\frac{4.988}{3.682} = 1.36$	$\frac{4.194}{3.289} = 1.28$	$\frac{5.04}{3.633} = 1.39$	$\frac{5.5}{4.3} = 1.28$	$\frac{4.585}{2.845} = 1.61$	$\frac{3.28}{2.72} = 1.21$	$\frac{4.28}{3.58} = 1.20$	$\frac{4.24}{3.52} = 1.21$
m3 L/Wa	$\frac{5.397}{3.325} = 1.62$					$\frac{3.81}{2.51} = 1.52$	$\frac{4.88}{3.38} = 1.44$	$\frac{4.75}{3.01} = 1.58$
m3 L/Wp	$\frac{5.397}{2.858} = 1.89$		$\frac{5.5}{3.4} = 1.62$		$\frac{4.285}{2.48} = 1.73$	$\frac{3.81}{2.22} = 1.72$	$\frac{4.88}{2.87} = 1.70$	$\frac{4.75}{2.50} = 1.90$

angular process is large and rounded, and it projects below the ventral border of the mandible. The inferior border of the mandible is inflected strongly medially on its posteromedial surface, below the fossa for the strong internal pterygoid musculature. On the medial surface of the mandible there is a weak, but distinct, mylohyoid crest; the inferior dental foramen (mandibular foramen) is elongate, and situated about at the level of the dental alveoli, midway between the posterior edge of m3 and the condyle; there is a strong crest (to which part of the superior constrictor musculature attaches in humans) lingual to the anterior margin of the ascending ramus; and there is a deep fossa anterior to the fossa for the internal pterygoid musculature, and extending forward to a point below the anterior border of m2, that presumably housed the submaxillary gland.

Lophodonty is well developed on the lower molars of *H. lovei.* The m1–3 hypoconulid is weak, but the entoconid is large and strong. A weak metastylid always is present on the posterior flank of the metaconid of m1–2. The m1 paralophid is relatively well developed.

In *H. lovei,* p3–4 are transversely broad and anteroposteriorly short (see tables 1 and 3). The trigonids are relatively broad transversely, and are not anteroposteriorly elongate. The p3–4 crown outline is trapezoidal or triangular, and there is a transverse expansion of the crowns just posterior to the protoconid apex. The talonids are very short anteroposteriorly, and the posterolabial margin of the talonid is oblique, rather than squared.

The p4 has a low L/W ratio (see table 3), indicating that the tooth is relatively broader than long. The paralophid is strong and oriented relatively straight anteroposteriorly. A broad slope or shelf is developed on the labial side of p4, labial to the paralophid and cristid obliqua. The posterior cingulum on the talonid is weak or absent.

The p3 is relatively short anteroposteriorly. The trigonid is weakly molariform; the paralophid is not particularly strong, and a metaconid is not elaborated as a distinct cusp. There is no lingual trigonid basining, and the labial flank of the trigonid is narrow and restricted transversely.

The p2 is short anteroposteriorly, and laterally compressed. The trigonid is dominated by a single large cusp, with sharp ridges running anteriorly and posteriorly from its apex. The talonid is very short, with a single anterocentral cusp.

The p1 is represented only by a small alveolus.

The anterior premolar dentition is closely appressed and anteroposteriorly compressed. All the anterior premolars are closely spaced and appear "cramped" in profile.

The lower incisors are compressed and closely appressed; there is little interstitial space between the incisors. The i1–2 are procumbent, and in lateral profile i1–2 are in the same position (i1 internal to i2) rather than i1 being located anterior to i2 on the mandible. In dorsal view, i1–2 form a squared, linear dental battery. Rather than being aligned in a broadly arcuate manner, i1 lies directly medial to i2, and the anterior edges

Fig. 3. AMNH 116454. Right mandible, i2–3, p2–m1. Crown view. 6.9×.

TABLE 4
Ratios of Length/Width for Upper Dentitions of Species of *Hyopsodus*

	lovei (1)	*uintensis* (2)	*sholemi* (3)	*minusculus* (4)	*paulus* (5)	*lepidus* (6)
P3 L/W	$\frac{3.084}{3.697} = 0.83$					
P4 L/W	$\frac{3.171}{5.210} = 0.61$	$\frac{3.066}{5.1} = 0.60$	$\frac{3.4}{5.6} = 0.61$	$\frac{1.95}{3.50} = 0.56$	$\frac{3.00}{4.58} = 0.66$	$\frac{2.70}{4.24} = 0.64$
M1 L/Wa	$\frac{4.426}{5.655} = 0.78$			$\frac{3.80}{5.08} = 0.75$	$\frac{4.18}{5.29} = 0.79$	$\frac{3.74}{4.88} = 0.77$
M1 L/Wp	$\frac{4.426}{5.452} = 0.81$	$\frac{4.368}{5.363} = 0.81$	$\frac{5.066}{6.466} = 0.78$	$\frac{3.80}{5.27} = 0.72$	$\frac{4.18}{5.13} = 0.82$	$\frac{3.74}{4.75} = 0.79$
M2 L/Wa	$\frac{4.679}{5.790} = 0.81$			$\frac{3.20}{4.40} = 0.73$	$\frac{4.37}{6.25} = 0.70$	$\frac{4.01}{5.67} = 0.71$
M2 L/Wp	$\frac{4.679}{5.599} = 0.84$	$\frac{4.538}{6.213} = 0.73$	$\frac{5.066}{7.333} = 0.69$	$\frac{3.20}{3.90} = 0.82$	$\frac{4.37}{5.90} = 0.74$	$\frac{4.01}{5.34} = 0.75$
M3 L/Wa	$\frac{3.700}{4.872} = 0.76$	$\frac{3.656}{5.191} = 0.70$	$\frac{4.025}{6.325} = 0.64$	$\frac{2.40}{3.50} = 0.69$	$\frac{3.56}{5.21} = 0.68$	$\frac{3.05}{4.54} = 0.67$
M3 L/Wp	$\frac{3.700}{4.718} = 0.78$					

of the incisors are transversely linear. The close appression and alignment of the incisors results in a squared dental arcade that appears "shovel-like" or "platform-like" in dorsal view.

In general, the incisors of *H. lovei* are spatulate. Both i1–2 are laterally broad, and the anterior surfaces of the teeth (in cross section) are broad and flat. There is a strong central ridge on the posterior (lingual) crown of i1–2 and there is a well-developed lingual basal cingulum on i2. The i2 has a lateral (external) shoulder, or projection, that is most obvious when viewed from the anterior and ventrally.

The wear pattern on the incisors of *H. lovei* is quite distinctive. Wear surfaces are concentrated on the apical and posterior (lingual) crown surfaces of i1–2. On the most anterior end of the crown of i2 the internal edge wears more heavily than the external edge. In dorsal view, this results in sharp lateral projections on the anterior surface of i2, and a somewhat concave (anteriorly) wear surface. The anterior surface of i1 exhibits slightly greater wear on the internal edge of the tooth, and the wear surface is also concave anteriorly. The wear surfaces of the incisor battery (from the left i2 to the right i2) are broadly continuous, and broadly concave anteriorly. The wear surface on i2 can be traced from the external half of the tooth on its posterior (lingual) surface, toward the internal edge of the tooth at its apex, and onto the internal half of the anterior (labial) surface. There is very little wear

Fig. 4. AMNH 96264. Right mandible, p2–m3, alveoli for i3, c, p1. Crown view. 4.9×.

Fig. 5. AMNH 114057. Right mandible, p2–m3. Crown view. 4.9×.

on the internal edge of the posterior (lingual) crown surface of i2. Dental measurements for *H. lovei* are provided in tables 1–2.

DISCUSSION: An hypothesis of phylogenetic relationships for *Hyopsodus lovei* and other species of *Hyopsodus* is presented in figure 10; The Phylogeny of *Hyopsodus* section (below) lists proposed derived characters for the taxa in figure 10. Although many dental characters vary gradationally between species, some derived features are discrete and can be used to diagnose species and clades. *H. lovei* shares several derived features with *H. uintensis* and *H. sholemi,* lacks some derived features of those two species (and, therefore, shares primitive features with *H. paulus* and some other Bridgerian and Wasatchian species), and has several features that are uniquely derived. The lower incisor dentition in *H. lovei* is quite specialized in comparison to the primitive "condylarthran" condition (compare to Gazin, 1968, and description for *H.* sp. cf. *H. paulus,* below) and clearly distinguishes *H. lovei* from all other species of *Hyopsodus.* The mandibular morphology of *H. lovei* also is distinctive, as it is more robust and proportionally shorter than in other species of *Hyopsodus.* There also is a stronger crest (probably for attachment of part of the superior constrictor musculature) lingual to the anterior margin of the ascending ramus than in other described species of *Hyopsodus* (see Gazin, 1968). The diagnosis for *H. lovei* details the morphological differences between this species and all other species of *Hyopsodus.*

Hyopsodus lovei shares with *H. uintensis* and *H. sholemi* the derived features of a reduced m1–3 hypoconulid; a broad postcingulum and strong preprotocrista on P3–4; an angular, squared outline of the upper molars; a large M1–2 hypocone; and well-developed molar lophodonty (see Krishtalka, 1979 for a discussion of these features in the latter two species). *H. paulus* and all other Bridgerian and Wasatchian species of *Hyopsodus* lack these derived morphological features as well as the derived features diagnostic of *H. lovei. H. lovei* further differs from those species in several dental proportions (see tables 3–4), including (1) lower P4 L/W ratio, indicating a more rectangular, transversely broad P4; (2) higher m2 length/trigonid width, indicating a more rectangular m2 with a relatively narrower trigonid; and (3) a higher M2–3 L/W ratio, indicating a more squared crown out-

Fig. 6. AMNH 104876. Left mandible, p2–m3. Crown view. 4.3×.

Fig. 7. AMNH 98084. Left maxilla, I2–3, C, P2–4, M1–3. Crown view. 6.3×.

line in *H. lovei.* Krishtalka (1979) cited a greatly enlarged m1–3 entoconid as a derived feature for *H. uintensis* and *H. sholemi.* In the material of *H. paulus, H. lovei,* and *H. uintensis* that I have examined in the collections of the American Museum of Natural History, the entoconid seems to be enlarged to about the same degree in all three species, and I cannot distinguish the species on the basis of this character.

Hyopsodus lovei differs from *H. uintensis* and *H. sholemi* in the lack of a paraconule on P4; triangular P3; strong connection of the M1–2 hypocone and protocone, rather than having a deep lingual valley that completely separates these cusps and that extends labially to the metaconule (as in *H. uintensis* and *H. sholemi*); smaller M3 hypoconal shelf; less reduced m1 paralophid; less molariform p3; and several metric size and length/width ratio differences (see tables 3 and 4) in *H. lovei.* In all of these features (except the size dimensions and ratios) *H. lovei* resembles *H. paulus* and other Bridgerian and Wasatchian *Hyopsodus.* These clearly are retained primitive features in *Hyopsodus lovei,* with respect to the derived condition in *H. uintensis* and *H. sholemi. H. lovei* further differs from *H. uintensis* in several metric size measurements and length/width ratios (see tables 3–4) including (1) anteroposteriorly longer m1 and P4–M3 and transversely wider p4–m2 and P4–M1; (2) transversely narrower M2–3; (3) smaller M1/m1 L/W ratio, indicating a more rectangular M1/m1; and (4) greater M2–3 L/W ratio, indicating a more square crown outline. Similarly, *H. lovei* differs from *H. sholemi* in having a larger M2–3 L/W ratio, indicating a more square crown outline in *H. lovei.*

Hyopsodus lovei has a distinct "swelling" on the preprotocrista of P4 in the region a paraconule is present in *H. sholemi.* Although Krishtalka (1979) cited a P4 paraconule as a

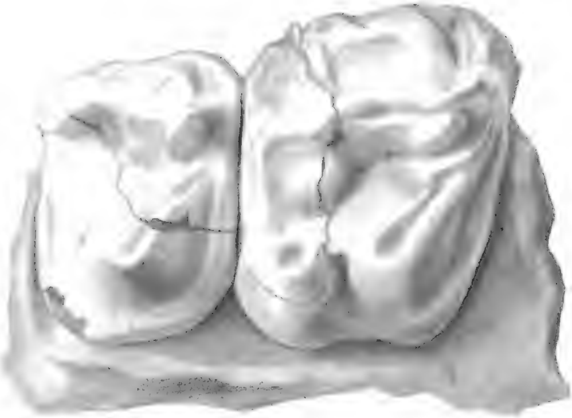

Fig. 8. AMNH 88290. Left maxillary fragment, M2–3. Crown view. 7.3×.

Fig. 9. AMNH 104876. ? Right mandible fragment, i2. Crown view. 7.1×.

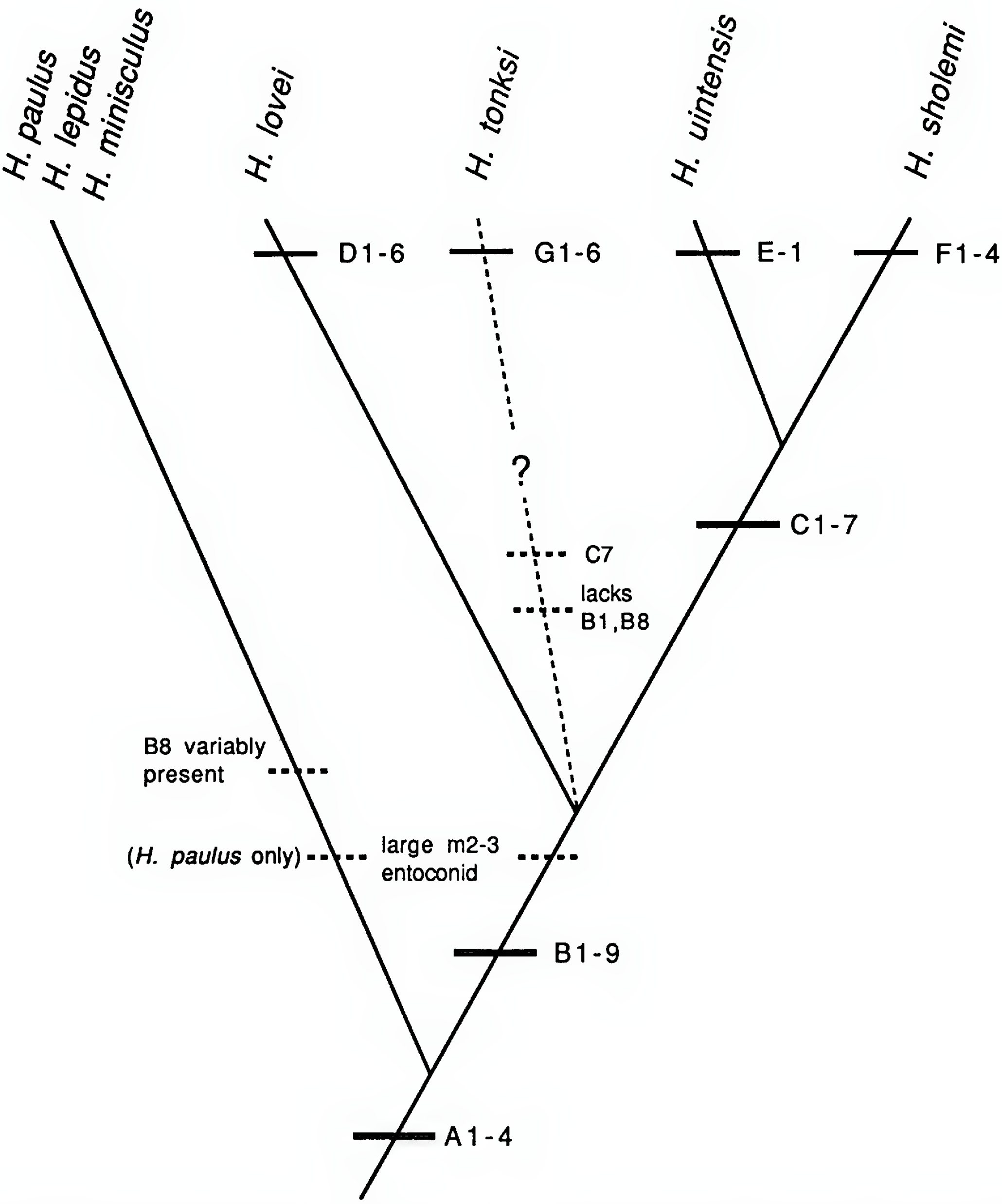

Fig. 10. Hypothesis of phylogenetic relationships of *Hyopsodus lovei.* Letters and numbers at nodes A–G indicate derived characters (solid bars), summarized in text, supporting monophyletic groups. Conflicting characters (homoplasies) indicated by dashed bars. *H. lovei, H. uintensis,* and *H. sholemi* form a monophyletic group within *Hyopsodus.* The relationships of *H. tonksi* are equivocal (indicated by dashed line with "?"; see text); *H. tonksi* shares several derived features with the *H. lovei* + *H. uintensis* + *H. sholemi* clade (node B), including characters B1 (but not as reduced), B5, and B6, but it lacks several synapomorphies of that clade (e.g., B8, B1 not as reduced). *H. tonksi* may share more oblique molar trigonids (C7) with *H. uintensis* + *H. sholemi* alone, but the condition in *H. tonksi* is unusually elaborated, and it is unclear whether this is a synapomorphy or convergence between *H. tonksi* and the other two species.

derived feature for *H. uintensis*, AMNH 2078 (type of *H. uintensis*) does not appear to have a paraconule any better developed than the "swelling" exhibited by *H. lovei*.

Hyopsodus lovei consistently has a weak metastylid developed on the posterior flank of the m1–2 metaconid. *H. uintensis* also has a weak metastylid consistently present on m1–2, and this cusp is very strong in *H. sholemi*. A metastylid on m1–2 first appears early in the phylogenetic history of *Hyopsodus*, but the earlier species have this cusp present only variably within a population sample. This cusp is absent in most *H. miticulus*, is weak and variably present in *H. paulus*, and is weak and more consistently present in *H. lepidus* from Tabernacle Butte, Wyoming.

Eaton (1982) recently described *H. tonksi* from the Bridgerian (?) Tepee Trail and Wiggins Formations, southeastern Absaroka Range, Wyoming, approximately 25–30 km north of the East Fork Basin area. *H. tonksi* is an unusually specialized species, with at least superficial resemblances to some notoungulates (Eaton, 1982). Its phylogenetic relationships are equivocal. If it is indeed a species of *Hyopsodus* it has many unique morphological features, including (1) extremely narrow and anteroposteriorly elongate lower molars, (2) more oblique trigonids and more angular lophids ("almost selenodont in appearance" Eaton, 1982: 183) than any other species of *Hyopsodus*, (3) presence of a small cusp on the anterior cingulum of m1 (in front of, and below, the metaconid), (4) parastyle wing on upper molars projecting far anterobuccally, (5) upper molars trapezoidal in outline rather than triangular or squared, and (6) the molar ectolophs high and wall-like. *H. tonksi* may share obliqueness of the molar trigonids with *H. uintensis* and *H. sholemi* (node C, fig. 10), but the condition in *H. tonksi* is extremely specialized and it is unclear whether this is an homologous synapomorphy or a convergent homoplasy between the taxa. Alternatively, *H. tonksi* may be a sister taxon to *H. lovei/uintensis/sholemi* (node B, fig. 10) based on the presence of a deep valley separating the molar hypocone and protocone (but with retention of a basal crest connecting these cusps, as in *H. lovei*), large hypocone, reduced m1–3 hypoconulid (relative to *Hyopsodus* that are sister taxa to taxa of node B), well-developed molar lophodonty, and possibly an enlarged molar entoconid. *H. tonksi* would be excluded from the clade of *H. lovei/uintensis/sholemi* because of its lack of a molar metastylid and presence of its relatively larger hypoconulid.

The difficulty in determining if *H. tonksi* even belongs within the genus *Hyopsodus* emphasizes that very few uniquely derived features diagnose and distinguish *Hyopsodus* from other early Cenozoic "ungulates" or "condylarths."

Uncataloged Carnegie Museum specimens from Loc. 1102, "Lake Beds" of the Wagonbed Formation (Eaton, personal commun., 1985; formerly the top of the Green and Brown Member, Tepee Trail Formation, Tourtelot, 1957), Badwater area, Wyoming, are similar to both *H. lovei* and *H. uintensis*. These specimens consist of two fragmentary lower molars and a complete p4. The teeth possess the derived features shared by the *H. lovei/uintensis/sholemi* clade, but the p4 lacks the diagnostic derived features of *H. sholemi*. The shape of p4 is particularly similar to that in *H. lovei* in the oblique posterolabial margin, broad slope on the labial side of the talonid, and anteroposteriorly short talonid.

Two uncataloged AMNH specimens from Loc. KS010, ?Early Uintan, Tepee Trail Formation, Owl Creek area, Wyoming (Sundell, 1982), are very similar to, and possibly referable to, *H. lovei*. One jaw preserves p4–m2, while the second jaw contains alveoli for p1–2, a fragmentary p3, casts of p4–m2, and a complete m3. These specimens share several derived features with *H. lovei* including the anteroposteriorly short, broad, triangular-shaped p4, and short p4 talonids with a broad labial slope and oblique posterolabial margin. However, the labial margin of the p4 talonid is more deeply invaginated than in *H. lovei*. The molars have well-developed lophodonty and reduced hypoconulids, and metastylids are present on m1–2 as in *H. lovei/uintensis/sholemi*. However, lophodonty is not as well developed and the trigonids are not as oblique as in *H. uintensis* and *H. sholemi*.

Many of the diagnostic features for distinguishing *H. lovei*, *H. uintensis*, and *H. sholemi* are characteristics of the upper dentition; upper teeth are not present in either the

Loc. 1102 or KS010 samples. I defer definite assignment of these specimens to species until more complete diagnostic material is available.

The uniquely derived features of *H. lovei* are summarized in the diagnosis and elaborated in the description section. *H. lovei* differs from all other *Hyopsodus* primarily in the shape and morphology of p3–4, several size and dimension differences in the dentition, and most obviously in the unique incisor battery present in this species.

Hyopsodus lovei is presently restricted, temporally and geographically, to the Shoshonian (earliest Uintan) of the East Fork Basin area of northwestern Wyoming. However, the specimens of *Hyopsodus* from the Tepee Trail Formation of the Owl Creek area (KS010, east of the East Fork Basin), and the uncataloged CM specimens from Badwater may also represent *H. lovei*. *H. lovei* is morphologically intermediate between *H. paulus/H. lepidus* and *H. uintensis* in many features. However, *H. lovei* clearly is distinguishable morphologically from these species on the basis of its distinctive, uniquely derived morphological features. Based on the distribution of derived features within *Hyopsodus, H. lovei* forms a monophyletic clade with *H. uintensis* and *H. sholemi,* and *H. paulus* is the taxon probably most closely related to this clade.

Hyopsodus lovei is of uncertain biostratigraphic or biogeographic use. Our current knowledge of *H. lovei* indicates it had a short temporal range (limited to Shoshonian Subage, Earliest Uintan Land Mammal Age), and might be useful for biochronologic correlation. However, the restricted geographic range of this species limits its present use for temporal correlation to northwestern Wyoming. It is important to note that *Hyopsodus* cf. *H. paulus* and *H. lovei* have mutually exclusive stratigraphic distributions in the East Fork Basin area. *Hyopsodus* cf. *H. paulus* is not present in the large sample of taxa from the Bone Bed A quarry, indicating that this species was probably not living in this area during the earliest Uintan. The presence of *H. paulus* in the early Uintan elsewhere (Krishtalka, 1979), and the recognition of *H. lovei* as a new, morphologically unique (and possibly very specialized in its dietary requirements—as reflected in the incisor specializations) species restricted to the southeastern Absaroka Range, supports the proposed ecologic uniqueness of the East Fork Basin area during the earliest Uintan (see McKenna, 1980; and Flynn, 1986).

Hyopsodus sp. cf. *H. paulus* Leidy, 1870

Referred Specimens: AMNH 104751 (left ramus with symphysis and part of right ramus, left i1–p2, p4–m2, right i1–c1); AMNH 104752 (right ramus with p4–m2).

Locality: Flynn's Folly Locality, Tepee Trail Formation, East Fork Basin, Center of SE¼, NW¼, SW¼, NW¼ section 4, T. 43 N., R. 104 W., Fremont County, Wyoming.

Discussion: The two specimens were found in immediate association with each other and with several isolated lizard scutes. The microstructure of the surrounding matrix, the breakage of the dental material, and the manner of association of the mammalian and reptilian remains all suggest that the small nodule in which they were found is a preserved coprolite of a carnivorous animal. Preservation within a coprolite documents the precise contemporaneity of these taxa. Such contemporaneity is rarely documented within the fossil record.

These specimens of *Hyopsodus* lie stratigraphically below the horizon of *H. lovei,* although the two levels are areally separated by only about a kilometer. Although the Flynn's Folly specimens are heavily worn, broken, and pitted, there are several distinctive morphological differences from the Bone Bed A *H. lovei*. These differences in *H.* sp. cf. *H. paulus* include: the smaller size (see table 3); lack of incisor specializations; m1 relatively longer than wide (trigonid and talonid relatively narrower); p4 talonid narrower just posterior to protoconid apex; p4 more rectangular than triangular in outline, with the posterolabial margin of the talonid squared rather than oblique; and possibly a less closely appressed premolar dentition.

The incisor battery in *H.* sp. cf. *H. paulus* is broadly arcuate (in dorsal view); the incisors are not closely appressed, are relatively more vertically oriented, and in profile i1 is situated anterior to i2; the anterior surface of i1–2 is narrow and very rounded; wear on i1–2 is apical and on the anterior (buccal) surface

of the tooth, with wear evenly distributed on both the medial and lateral edges of the apices of the incisors; i2 lacks a lateral (external) expansion or "shoulder" at the base of the crown, and has only a weak lingual (posterior) basal cingulum; and i1–2 have only a weak central-lingual ridge on their posterior crown face. In all of these features *H.* sp. cf. *H. paulus* differs strongly from the derived condition found in *H. lovei* (described above), and closely resembles the primitive morphology exhibited by *H. minusculus* (USNM 24891, Blacks Fork Member (B), Bridger Formation, Green River Basin, Wyoming—see Gazin, 1968).

In absolute size the Flynn's Folly Locality specimens are much smaller than *H. lovei*, but are very close in size to *Hyopsodus paulus* from the Bridger Formation (see West, 1979). Although the p4 L/W ratio in these specimens is almost identical to that in *H. lovei*, the morphology of p4 is very different between the two species. In the narrow labial shelf of p4, narrower width of the p4 talonid just posterior to the protoconid apex, more rectangular p4 outline, and squared posterior talonid margin and lack of a posterolingual flare of the talonid of p4, and the general dimensions of p4–m2, the Flynn's Folly specimens more closely resemble *H. paulus* than any other known species. The relatively well-spaced premolar dentition found in all Bridgerian, and older, species of *Hyopsodus* also appears to be exhibited by the rami in the Flynn's Folly specimens (although no premolar crowns anterior to p4 are preserved). The extremely heavy wear on these specimens precludes any determination of the relative size of the entoconids, degree of lophodonty, or size of the hypoconulids in the molars. These features are used in distinguishing *H. lovei, H. uintensis,* and *H. sholemi* from all other species of *Hyopsodus* (see above; and Krishtalka, 1979).

Based on the size and morphology of the Flynn's Folly *Hyopsodus* specimens, I exclude them from *H. lovei,* and I tentatively exclude them from *H. uintensis* (larger size, incisors unknown) and *H. sholemi* (much larger size, very different p4 morphology and p4 and m2 dimensions, incisors unknown). Many of the unique features for *H. uintensis* and *H. sholemi* are features of the upper dentition; no upper dentitions are preserved for the Flynn's Folly specimens, for comparison. I tentatively assign these specimens to *Hyopsodus* sp. cf. *H. paulus,* the species to which it is most similar in morphology.

H. paulus has a temporal range from early Bridgerian (middle Bridger B strata) to early Uintan (White River Pocket, Uinta B strata), according to the work of West (1979, especially p. 16) and Krishtalka (1979, especially p. 383). If the specimens from the Flynn's Folly Locality can be truly assigned to *H. paulus,* they indicate an age of somewhere between early Bridgerian and early Uintan for this stratigraphically lowest faunal horizon in the Tepee Trail Formation of the East Fork Basin. Such an age assignment is consistent with the Bridgerian and earliest Uintan ages of the faunas bracketing this horizon (Flynn, 1986), but the relatively broad temporal range of *H. paulus* does not aid in determining a more precise age for the lower part of the Tepee Trail Formation in this area.

Phylogeny of *Hyopsodus*

The following list of characters abstracts the features that are assumed to be derived for members of each taxon or clade. The nodes are those given in the phylogeny of figure 10:

Node A (from West, 1979: 5): *H. minusculus, H. lepidus, H. paulus, H. lovei, H. uintensis, H. sholemi,* and possibly *H. tonksi* ["Post-Wasatchian" *Hyopsodus*]

1) large P3 protocone
2) well-developed hypocone on M1–2, variable on M3
3) distinct crest uniting M1–2 hypocone and protocone (also present in late Wasatchian species)
4) distinct molar conules
5) M2 generally much larger than M1
6) general increase in angularity and lophodonty
7) incipient trigonid on p3
8) more complete development of trigonid on p4
9) no paraconid on m1–3, thereby eliminating the trigonid basin and increasing "angularity" of the trigonid
10) distinct molar entoconid

11) broad molar talonid basin which opens lingually
12) well-developed median molar hypoconulid
13) small, variably developed molar metastylid
14) no molar entostylid

NODE B: *H. lovei, H. uintensis,* and *H. sholemi*

1) reduced m1–3 hypoconulid
2) broad postcingulum, strong preprotocrista on P3–4
3) angular, squared outline of upper molars
4) higher-crowned upper molars with more trenchant cusps and stronger, sharper, more "wall-like" external lophs
5) large M1–2 hypocone
6) deep lingual valley separating molar hypocones and protocones, but presence of basal crest connection retained
7) well-developed molar lophodonty
8) m1–2 metastylid consistently present (variably present in other species)
9) molariform p4
10) less oblique labial tooth margin on M3

NODE C: *H. uintensis, H. sholemi*

1) paraconule on P4 (Krishtalka, 1979; but the type specimen of *H. uintensis* has a swelling, not a paraconule, that is no larger than in *H. lovei*)
2) rectangular P4
3) no basal crest connecting molar protocones and hypocones, and deep lingual valley extends labially to metaconule
4) large M3 hypoconal shelf
5) very reduced m1 paralophid
6) broad, molariform p3; strong p3 paralophid
7) more oblique molar trigonids

NODE D: *H. lovei*

1) closely appressed antemolar dentition
2) short, robust mandible
3) broad, anteroposteriorly short, more triangular (in outline) shaped p3–4 with very short (anteroposteriorly) talonids and transversely expanded tooth crowns just posterior to the protoconid apex
4) relatively broader than long p4, much lower length/width ratio
5) broad slope or shelf on the labial side of p4 (labial to the centrally located paralophid and cristid obliqua)
6) oblique, rather than squared, posterolabial margin of p4 talonid
7) development of an unique incisor dental battery

NODE E: *H. uintensis*

1) lingual basining of p3 talonid

NODE F: *H. sholemi*

1) distinct metaconid always present on p3; stronger p3 paralophid; p3–4 more molariform
2) m1–2 metastylid strong
3) P3 more molariform, quadrate in outline, expanded postcingulum
4) much larger than any other described species of *Hyopsodus*

Incertae sedis: NODE G: *H. tonksi*

1) extremely narrow and anteroposteriorly elongate lower molars
2) more oblique trigonids and more angular lophids than any other species of *Hyopsodus*
3) presence of a small cusp on the anterior cingulum of m1
4) parastyle wing on upper molars projects far anterobuccally
5) upper molars trapezoidal in outline
6) molar ectolophs high and wall-like

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